Microbial Ecology and Decomposition in Arctic Tundra and Subarctic Taiga Ecosystems

P.W. FLANAGAN

A. Introduction

Northern forest sites have low decomposition rates (K) while those further south and in tropical areas have higher K values (3, 14, 16). It has been suggested that in arctic tundra ecosystems litter is decomposed at very slow rates resulting in organic accumulation and in a depauperate N, P, and K available nutrient pool (8). Some workers suggest that decomposition processes are slowed by the adverse climatic conditions of northern climes more than are primary production processes (2, 13, 15, 16, 20); which fits the observation that there is more accumulation of dead organic matter in some northern ecosystems compared with southern systems. The concept has consequently developed that northern ecosystems in general are limited functionally by climatically-controlled immobilization of microbial activities, organic remains and essential nutrients.

There is no clear indication however from field data and decomposition studies on tundra areas that northern ecosystems are accumulating organic matter. The present assessment of annual decay rates at Pt. Barrow, Alaska is very close to the measure of total net annual primary production (9). Whether or not decomposition is quicker in warmer than in colder climates is not in question. The question is whether the balance between decomposition and primary productivity changes with latitude, and if so, are decay rates lagging production rates in the colder climates? If primary producer activity decreases with decreasing temperature are secondary production and decomposition processes amongst microorganisms proportionally more limited by low temperatures? This situation would imply that microorganisms are less cold tolerant and/or cold adaptable than are producer cryptogams and phanerogams.

The present study was undertaken seven years ago to examine if microorganisms in northern ecosystems function at low temperatures at rates as high as those of temperate organisms at their respective habitat temperatures. It was of particular interest to see if psychrophilism was prevalent in microorganisms of northern ecosystems and if northern ecosystem microorganisms could recycle enough organic matter each year to balance annual organic matter production.

B. Study Sites

The tundra sites at Eagle Summit and Pt. Barrow have been described (1, 5) as has the spruce forest site (10). A fifth site in a stand of paper birch Betula papyrifera included in this study was on the campus of the University of Alaska, Fairbanks and, is underlain by fine silty loess soil on top of birch creek schist of precambrian age. Alnus sp. intermingle with the dominant trees and Calamagrostis sp. prevails in open areas while the entire forest floor is covered in summer by a carpet of Equisetam arvense. Patches of Hylocomium splendens occur amongst the Equisetum especially close to stem bases.

C. Methods

Fungal and bacterial biomass was estimated using described (12) modified (10, 19) methods. Fungi were isolated (17) on potato dextrose agar and malted soil extract agar. Fungi from temperate ecosystems (peat bogs) were provided by Pamela Latter, Institute of Terrestrial Ecology, Merlewood, Cumbria, UK., and by Dr. Paul Dowding, Trinity College, Dublin and isolations were made (17) in Western Ireland.

Decay rates were measured by inserting indigenous plant remains and cellulose strips in litter bags into the upper 10 cm of organic soil. Bags were collected for reweighing each year for 3 years.

NH_4^+, NO_2^- and NO_3^- were estimated using publicised methods (4) and available P after ammonium fluoride extract and by the molybdenum blue method.

The effect of temperature on growth of selected isolates was determined by measuring increase in weight of mycelium on following incubation at 5 degree intervals from -5°C to 55°C at specific times. Yield of mycelium (grams/fungus/gram substrate) and fungal respiration at different temperatures was measured in mineral vitamin solution with added glucose in Gilson respirometers (8, 10).

Only those fungi able to grow optimally at or below 20°C were considered truly psychrophilic (11). Those able to metabolise at or below 0°C and with growth optima in the 25°C-35°C range were designated cold tolerant mesophiles. Organisms unable to grow below 2°C with optimal metabolic activity in the 30°C-40°C range were considered true mesophiles. Ten representative organisms of each of the above categories, grown from single spores or single 3-5 mm lengths of hyphal tip obtained from liquid potato dextrose culture, were placed in mineral salt-vitamin solution for measurement of their growth, respiration and yield (7, 8, 10). Growth, yield coefficients, and respiration of some major fungal species from latitudinally separated research regions were also determined at a variety of temperatures (7, 8, 10). Respiration rates in root-free organic remains from the upper 10 cm of organic soil were monitored at a variety of temperatures (8, 10) to establish the optimum temperatures for microbial activity by site and for comparison with measure of decay in litter bags.

D. Results and Discussion

Bacterial biomass (direct counts) never constituted more than ten percent of the total microbial biomass in any of the study areas. Fungi were the predominant decomposers in all sites. On the average, live hyphae accounted for 70%, 65%, 85% and 50% of all hyphae at Eagle Summit, Pt. Barrow, the birch forest and spruce forest respectively.

No significant differences in metres (m) of live mycelium g^{-1} organic matter were detected between tundra and birch sites, but spruce forest had significantly fewer m. of live hyphae (Table 1).

No significant difference was observed between sites in the rate of cellulose decay. The levels of annual decay were lowest in the spruce forest and equally higher in the birch and tundra sites (Table 1). Organic matter and litter of the latter sites had similar and higher readily extractable fractions (in hot water and 80% ethanol) than the spruce litter materials. The tundra sites were very much richer in soluble N and P than the two forest sites despite the relatively higher decay rate in the birch forest. Barrow tundra had 2 and 4 times more organic matter than the birch and spruce sites respectively (Table 2).

Of 38 and 36 fungal isolates 22% and 10% were psychrophilic at Pt. Barrow and Eagle Summit respectively, and 55% and 10% of fungi in these sites were cold

Table 1. Annual Decomposition and Productivity of Fungi and Plants

Site	Decomposition* $g\ m^{-2}\ y^{-1}$	% wt loss cellulose	$\bar{x}$ m. live mycelium per g organ-matter	calculated microbial productivity $g\ m^{-2}\ y^{-1}$	measured primary productivity $g\ m^{-2}\ y^{-1}$	annual microbial yield per g primary productivity	Indicated rate of organic accumulation $g\ m^{-2}\ y^{-1}$
Eagle Summit	235	3.4±5	570	133	203 (a)	.57	-5
Pt. Barrow	310	3.3±4	650	141	275 (b)	.56	-35
Birch forest	350	5.2±1.3	580	178	375 (c)	.51	+25
Spruce forest	198	3.4±1.0	300	117	180 (d)	.65	-18

* Litter bags inserted in litter layer and at 5-10 cm depth

(a) (1)

(b) (5)

(c) Litter tray data

(d) 1977 estimate, taiga biome colleagues

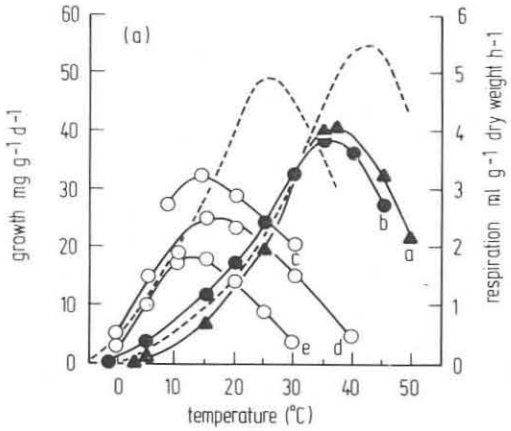
Table 2. Site organic matter and nutrient content

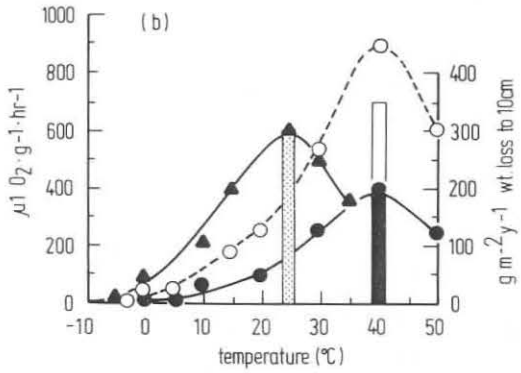
Site	Kg m^{-2} organic matter to 10 cm	% of organic matter readily extractable*	mg m^{-2} soluble-extractable N	P
Eagle Summit	10.5	14.5	118.5 (a)	7.4 (a)
Pt. Barrow	18.0	13.5	3600.0 (b)	22.0 (b)
Birch forest	4.3	14.8	.422	.190
Spruce forest	8.6	2.5	.156	.095

* Warm water followed by 80% Ethanol

(a) (1)

(b) (6)





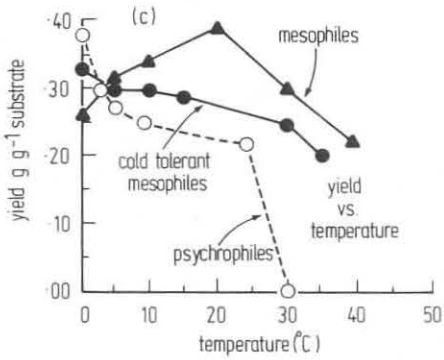


Fig. 1. (a) Fungal growth (solid lines) and respiration (fractured lines) vs. temperature. a Mesophilic fungi (average of 10 different species typified by (Rhizopus stolonifera). b Same for cold tolerant mesophiles typified by Cladosporium herbarum. c-e Psychrophilic fungi, Cylindrocarpon magnusianum, Mycelium sterilium and Chrysoporium pannorum respectively. (b) Annual amount of decay and respiration vs. temperature in tundra (▲ ▨), taiga birch (o □), and spruce (● ■) forests. (c) Fungal yield vs. temperature. Points represent the average reading for 10 representative organisms in the categories shown on the figure

tolerant mesophiles. The remainder were mesophilic. Spruce and birch forest mycoflora were composed of 40% mesophilic and 60% cold tolerant mesophilic fungi. Only one psychrophilic form was isolated in these taiga sites.

Decomposer microorganisms in the organic remains of tundra sites respired optimally at 25°C while those of taiga forest floors had optimum respiratory activity above 40°C. (Fig. 1 (b)). Optimum temperature for growth of major species components from these sites was 15°C and 35°C respectively. The low temperature thresholds for respiration and growth of major tundra psychrophilic fungal components was -6°C and 20°C while for taiga cold tolerant fungi they were 0°C and +3°C. (Fig. 1 (a)). Yield of fungal tissue (g fungus/g substrate) was higher at low temperatures than at optimum growth and respiration temperatures for all organisms tested (10 in each of the categories psychrophilic, cold tolerant mesophilic and mesophilic) (Fig. 2). Optimum temperatures for growth respiration and yield differed for each individual organism and markedly between the temperature related categories: psychrophiles, mesophiles and cold tolerant mesophiles (Fig. 2 (a)). Fungi from temperate European sites were all mesophilic. No cold tolerant or psychrophilic forms occurred amongst the temperate site species screened.

Calculated microbial productivity varied significantly between sites. The primary productivity: microbial productively ratio however was similar between sites. The spruce forest fungal productivity was lowest but in relation to primary productivity was highest (Table 1).

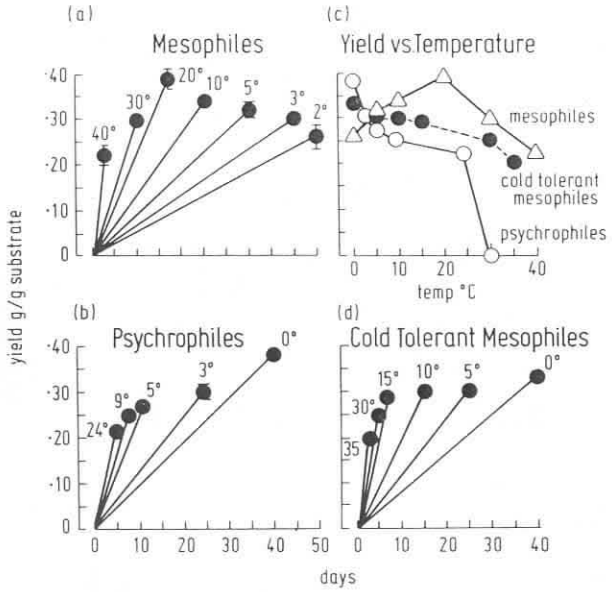


Fig. 2 a-d. Fungal yield (g fungal tissue / g available substrate) at various temperatures and times. Solid points on (a, b and d) represent the average reading for 10 representative organisms in the respective categories. I represents the standard error of the means for the 10 isolates. Where I is not shown standard error is at limit of •. In (c) a collage, all data for all isolates in each category are represented by individual curves

Annual amount of decay was highest in the birch forest but the level of decay was not much above those measured in tundra sites where consistently the annual level of decay was as high or higher than the measured annual primary productivity at the sites (Table 1).

Except for the birch site data, there is no indication of accumulation of organic matter in any of the ecosystems. Accumulated organic matter is highest in the tundra sites, lowest in the birch forest and of intermediate level in the spruce forest.

The discrepancy between the measures of annual net primary productivity and decay of organic matter is small and due, no doubt, to the margin of error implicit in the techniques used to measure and calculate productivity and decomposition. Still there is reasonable argument that microbial decay processes and productivity in these northern ecosystems are quite capable of balancing the input to the systems from primary productivity. It would appear, then, that the ecosystems studied are in, or very close to, a steady state.

The lower fungal biomass in organic remains in the spruce forest floor is reflected in the lower respiration rate in these substrates and in their lower annual decay rates. Because of the similarity in temperature responses of mycoflora from spruce and birch forest floors, similarity of location and the low levels of available N and P in both, it may be interpreted that lower decay rates in the spruce forest floor are not related primarily to low temperature attenuation of decomposers or nutrient deficiency but are more likely related to the low quality of spruce forest litter where the readily available carbon compounds are very low (Table 2) and the content of lignocellulose, waxy compounds, and moss remains is high.

Psychrophilic and low temperature tolerant fungi in the tundra are clearly responsible for the rates of decay in tundra sites where the mean annual temperature is below - 10°C (5).

The contour of the growth and respiration vs. temperature curves in tundra psychrophilic fungal species shows them functioning optimally at 15°C and 25°C respectively and their rate of activity is markedly higher than that of cold tolerant and temperate mesophiles in the same temperature range. The combination of cold tolerant and psychrophilic fungi in tundra assures efficient decay at temperatures where mesophilic fungi would barely metabolize and allows advantage to be taken of short periods when temperatures are relatively high.

Because exponential responses to temperature change show that the rate of positive response to temperature increases at higher temperatures, the linear response of psychrophiles to temperature increases at low temperature suggests special adaptations to low temperatures. At low temperatures, psychrophilic fungi attain higher maximal yields at faster rates than cold tolerant and temperate mesophiles. Psychrophilic forms, however do not have as efficient yield from substrates above 5°C as cold tolerant and temperate mesophiles. It appears that psychrophiles are adapted to maximise retention of energy at very low temperatures; an adaptation with obvious survival value.

The marked difference between optimal temperature for respiration, and that for growth is in keeping with the variation in yield at different temperatures (Fig. 2). Apparently, in northern ecosystems, as temperatures decline more of the substrate is converted to biomass and as temperatures increase less is used in biomass produdction irrespective of whether an organism is psychrophilic or a cold tolerant mesophile. The mesophilic fungi attain maximum yield potential at 20°C and decline in efficiency as temperatures increase or decrease. These observations are of importance in calculation of annual microbial productivity within and between ecosystems.

Annual microbial productivity should be calculated based on some average biomass estimate, substrate availability and integration of known temperature/yield relationships across the site annual temperature transient.

Optimum temperatures for mesophilic activity (35°C-45°C) rarely occur in temperate field sites, in fact temperatures above 25°C are rare whereas in northern ecosystems field temperatures especially in the upper soil surfaces are frequently in the 15°C-20°C range. In this temperature range psychrophilic fungi and cold tolerant mesophiles function at higher rates than mesophilic fungi and the latter do not attain an equal rate of activity until temperature is in the 25°C-30°C range.

The question of whether northern latitude microorganisms metabolize (grow and/or respire) as fast at low temperatures as temperate ecosystem mesophilic microorganisms at higher temperatures can be answered. Mesophiles respire, grow and yield more at higher temperatures than psychrophiles at their preferred lower temperatures but neither at low or high temperature do they exceed the metabolic activities of cold tolerant mesophiles from northern climes.

The presence of the latter group of fungi together with psychrophiles assumes overall that microbial metabolism and decay processes proceed during the biokinetic season in northern latitudes at rates equal to those occurring in temperate ecosystems functioning at higher field temperatures. The biokinetic season in temperate ecosystems, however, is much longer than that in northern latitudes so that decay processes in the former continue throughout the year while in the latter they cease abruptly when soil temperatures reach -5°C. Nonetheless, microbial activity during the short season decreases organic matter sufficiently to balance the income from primary productivity.

These decay rates, mycofloral activities and the surprisingly high levels of available N and P in tundra soils contradict the view (18) that it is cold and nutrient deficiency that causes organic accumulation in tundra ecosystems. It also

appears that northern forest microorganisms recycle as much organic matter annually as is produced. Low decay rates of organic matter on spruce forest floors in this study are attributed to their low chemical quality. Accumulated organic matter in northern ecosystems may not be associated with imbalances between decay and production rates but reflect the degree and/or duration of imbalances that occurred during the period preceding the attainment of steady state.

E. Acknowledgements

Without the data and time freely given by my colleagues in the U.S. Tundra Biome and taiga forest studies this paper would not have been possible. Special thanks are due to Drs. S.F. MacLean Jr., Robert White and F. Stuart Chapin III for critical discussion of the study approach, and field data. Research was financed partially by National Science Foundation Grants BMS 75-13998, and 9V29342 both to the University of Alaska to support the taiga forest research program and the U.S. Tundra Biome program respectively.

F. References

1. Anderson, J.H.: Plants, Soils, Phytocenology and Primary Productivity of the Eagle Summit Tundra Biome Site. U.S. Tundra Biome Data Report 74-42 pp. 211, (1974).
2. Bell, M.K.: Decomposition of herbaceous litter. In: Biology of Plant Litter Decomposition. Vol. 1 C.H. Dickinson and G.J.F. Pugh (ed.). Academic Press, New York. pp. 37-67 (1974).
3. Bray, J.R. and E. Gorham.: Litter production in forests of the world. In: Advances in Ecological Research, G.B. Gregg, (ed.). p. 101-152, (1964).
4. Bremner, J.D.: In: Methods of Soil Analysis. Vol. 2. C.A. Block (ed.), American Soc. Agronomy publication, Agronomy 9. (1965).
5. Bunnell, F.L., MacLean, S.F. Jr. & Brown, J.: Barrow, Alaska U.S.A. In: Structure and Function of Tundra Ecosystems. T. Rosswall and O.W. Heal (eds.) Ecol. Bull. (Stockholm) 20: 73-124 (1975).
6. Chapin, E.F. III, Miller, P., and Coyne, P.: Carbon and nutrient budgets, quantities and turnover rates. Chap. 19. In: An Arctic Ecosystem: The Coastal tundra of Northern Alaska, Brown et al., (eds.). Dowden Hutchinson and Ross. Stradsburgh, Pa. (1977). (In Press).
7. Flanagan, P.W.: Physiological groups of decomposer fungi. In: The Fungal Community. D.T. Wicklow & G.C. Carroll, (eds.). Marcel Dekker Inc., New York. (1977). (In Press).
8. Flanagan, P.W. & Bunnell, F.L.: Decomposition models based on climatic variables, substrate variables, microbial respiration and production. In: The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. J.M. Anderson & A. Macfadyen (eds.). Blackwell Sci. Publ. p.437-457 (1976).
9. Flanagan, P.W. & Bunnell, F.L.: Microbial activities and decomposition. In: Arctic Ecosystem: The Coastal Tundra of Northern Alaska. J. Brown et al., (eds.). Dowden, Hutchinson and Ross, Inc. Stradsburgh, Pa. (1977) (In Press).
10. Flanagan, P.W. & Van Cleve, K.: Microbial biomass, respiration and nutrient cycling in a black spruce taiga ecosystem. In: Soil Organisms as Components of Ecosystems. U. Lohm, (ed.). Ecol. Bull. (Stockholm). 23: (1977) (In Press).
11. Griffin, D.M.: Ecology of Soil Fungi. Syracuse Univ. Press. 193pp. (1972).

12. Hanssen, J.F., Thingstad, T.F., & Goksoyr, J.: Evaluation of hyphal lengths and fungal biomass in soil by a membrane filter technique. Oikos 25, 102-107 (1974).

13. Heal, O.W. & French, D.D.: Decomposition of organic matter in tundra. In: Soil Organisms and Decomposition in Tundra. A.J. Holding et al., (eds.). IBP Tundra Biome Steering Committee. Stockholm, pp. 279-310 (1964).

14. Jenny, H.W., Gessel, P., & Bingham, F.T.: Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68, 419-432 (1949).

15. MacLean, S.F. Jr.: Primary production decomposition and the activity of soil invertebrates in tundra ecosystems: A hypothesis. In: Soil Organisms and Decomposition in tundra. A.J. Holding et al., (eds.). IBP Tundra Biome Steering Committee. Stockholm, p. 197-206 (1974).

16. Olson, J.S.: Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44 (2), 233-331 (1963).

17. Parkinson, D. & Williams, S.T.: A method for isolating fungi from soil microhabitats. Plant and Soil 13 (4), 347-355. (1961).

18. Rodin, L.E. & Baszilevich, N.J.: Production and Mineral Cycling in Terrestrial Vegetation. Oliver and Boyde, Edinburgh. pp. 288 (1967).

19. Trolldenier, G.: The use of fluorescence microscopy for counting soil microorganisms. Bull. Ecol. Res. Comm. (Stockholm) 17, 53-59. (1973).

20. Waksman, S.A. & Gerretsen, F.C.: Influence of Temperature and Moisture upon the Nature and Extent of Decomposition of Plant Residues by Microorganisms. Ecology 12 (1), 33-60 (1931).